Research Article

Rapid expansion and facilitating factors of the Ponto-Caspian invader *Dikerogammarus villosus* within the eastern Baltic Sea

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Abstract

Dikerogammarus villosus, an amphipod of Ponto-Caspian origin, has recently and rapidly spread along Baltic coastal lagoons and estuaries. By 2016 it had invaded Russian (Kaliningrad region), Lithuanian and Latvian waters, but was not recorded from Estonian waters. This species has a discontinuous distribution suggesting a "jump" was involved in its dispersal. A classification tree and GLM analyses confirm such an observed distribution pattern and suggest productivity of the environment, distance to the nearest lagoon/river mouth and distance to the nearest port/marina were the most influential explanatory variables of its distribution. Our data indicates this rapid east and northward expansion is very likely due to vessel transport, which would account for the "jump" dispersal. Other vectors facilitating further spread are almost certainly acting at a local scale such as overland transportation of vessels, movements of diving gear, drifting mats of algae, macrophytes and flotsam, as well as natural spread. We predict the "killer shrimp" will soon appear within the entire Gulf of Riga and the Gulf of Finland, and also expand up-rivers of the eastern Baltic Sea. Following the species expansion, alterations and changes to macroinvertebrate assemblages in invaded areas can be expected.

Key words: amphipod, invasive, spread, vessels, hulls, drift

Introduction

The Ponto-Caspian amphipod *Dikerogammarus villosus* (Sovinsky, 1894) is the only peracaridian crustacean included in the list of 100 worst alien species in Europe (DAISIE 2009). In invaded areas the species became known as the "killer shrimp" and has been repeatedly reported as a voracious predator capable of feeding on a wide range of moderate-sized prey (Dick and Platvoet 2000; Dick et al. 2002; Haas et al. 2002) including congeners (Müller et al. 2002), fish eggs and young fishes (Devin and Beisel

2009), juvenile crayfish (Buric et al. 2009) and also insects (Pöckl 2007). Consequently the "killer shrimp" can, and often did, cause declines of several invertebrates (Dick and Platvoet 2000; MacNeil et al. 2013) including native gammarids (Dick and Platvoet 2000), even damaging them without consuming them (Dick et al. 2002). In invaded regions it occurred in reservoirs, lakes (MacNeil et al. 2010; Yakovleva and Yakovlev 2010) and rivers (Haas et al. 2002), excluding both native and non-native species from habitats (Devin et al. 2003) and altering the structure of resident macroinvertebrate communities (van Riel et al. 2006). It has been suggested that the predatory nature of *D. villosus* in the field can be exaggerated as the species may largely rely upon primary production, as revealed using stable isotope analysis (Koester et al. 2016).

The amphipod *D. villosus* originates from the lower reaches of rivers and their estuarine and lagoon systems draining into the Caspian, Black and Azov seas (Mordukhai-Boltovskoi 1969; Bij de Vaate and Klink 1995). Initially, the "killer shrimp" spread upriver along the Danube, entering the Rhine by means of the Main Canal which was opened in 1992, and then to the lower Rhine in 1994 (Bij de Vaate and Klink 1995). This downriver spread leads to the colonisation of estuarine regions of the North Sea (Rewicz et al. 2014). The species also progressed *via* the inland waterways westward to French waters (Bollache et al. 2004) and eastwards to the Szczecin Lagoon in the Baltic Sea by 2002 (Gruszka and Woźniczka 2008). The "killer shrimp" also spread across a marine barrier to Britain (MacNeil et al. 2010). A further expansion route involved the Dnieper and Pripyat rivers and with connections to the Bug River spread to the Vistula River by 2007 (Bącela et al. 2008). Taking this Central invasion corridor, *D. villosus* appeared within the western Vistula Lagoon in 2011 (Dobrzycka-Krahel et al. 2015). The earliest record from the eastern Baltic coast was from the waters of Kaliningrad, Russia, in 2013 (Molchanova and Ezhova 2018), and at the sea entrance to the Vistula Lagoon (Gusev et al. 2017). It subsequently appeared in the Curonian Lagoon and estuary of the Šventoji River, Lithuania (Šidagytė et al. 2016).

This dispersal of *D. villosus* led to concerns of a further rapid expansion within the Baltic Sea and its basin, as well as to other regions including a possible spread with shipping to the Laurentian Great Lakes of North America, noted as a risk for some time (Ricciardi and Rasmussen 1998). However, Kramer et al. (2017) concluded its ability to colonise this North American region, based on a climate tolerance, was marginal. It also remains unclear how suitable are environmental conditions in the Baltic coastal and inland water for its further eastward and northward expansion.

We examined the current distribution of the amphipod *D. villosus* in the coastal and estuarine waters of the Baltic Sea, revealing the principal factors determining its distribution and predict the possible extent of its expansion within the eastern Baltic Sea.

Materials and methods

Sample collection and study sites

The presence of *D. villosus* was investigated in 2015, 2016 and 2017 for 72 sites in the eastern Baltic Sea. These were located in coastal and estuarine waters of the Kaliningrad Region, Russia (29 sites, which included some re-examined samples collected in 2013 and 2014), Lithuania (15), Latvia (24) and Estonia (4). All available data from Russia, Lithuania and Latvia were used in analyses. The Estonian dataset of 284 sites were without records of *D. villosus* for 2016. These sites were also devoid of the species in 2017. To reduce the role of these data in the statistical analyses (see below), the Estonian dataset was restricted to four sites (69–72, Figure 1), located in the Gulf of Riga where the species occurrence had the highest probability. This included two marinas located close to Latvian waters and two sites near ports.

Several methods were used to obtain specimens. Most macroinvertebrate samples, collected using a standard hand-net, included amphipods. Amphipods were also collected from drifting plants, wetsuits of divers and various submerged substrates: stones, timber, *Dreissena* druses, debris, and attached macrophytes, etc. Sampling in Latvian waters included the use of a baited trap. Along the Estonian coast and several sites along the Russian coast, frame samples usually deployed from the water level to the depth limit of macrophytes, were collected by divers.

Identification of *D. villosus* was based on the shape of the dorsal conical protuberances on urosomes I–II and the dense tufts of long setae on the flagellum of antennae II and on the propodus of gnathopods in males (Eggers and Martens 2004; Dobson 2012; Zettler and Zettler 2017). These keys feature the presence of 3–5 spines on each of the two dorsal protuberances of the urosome I–II. However, the material from Lithuanian (Šidagytė et al. 2016) and Latvian (*unpublished results*) waters clearly showed that normally two spines were present, although all other features conformed to that of *D. villosus*.

Analyses

Two statistical methods suitable for testing effects of multiple predictors on a single binary (presence/absence) dependent variable were used. First, a classification tree using the Brodgar, version 2.7.5, software (www.brodgar.com/index.php/download), was selected to explain the distribution of *D. villosus* in the analysis of the presence/absence data as a dependent variable. Environmental variables examined were: distance of the site from the nearest port (km) and position of the site in respect to port (categories "upstream", "downstream", "in the port"), distance to the mouth of the nearest river or lagoon (km), exposure category of a site ("exposed" for coastal
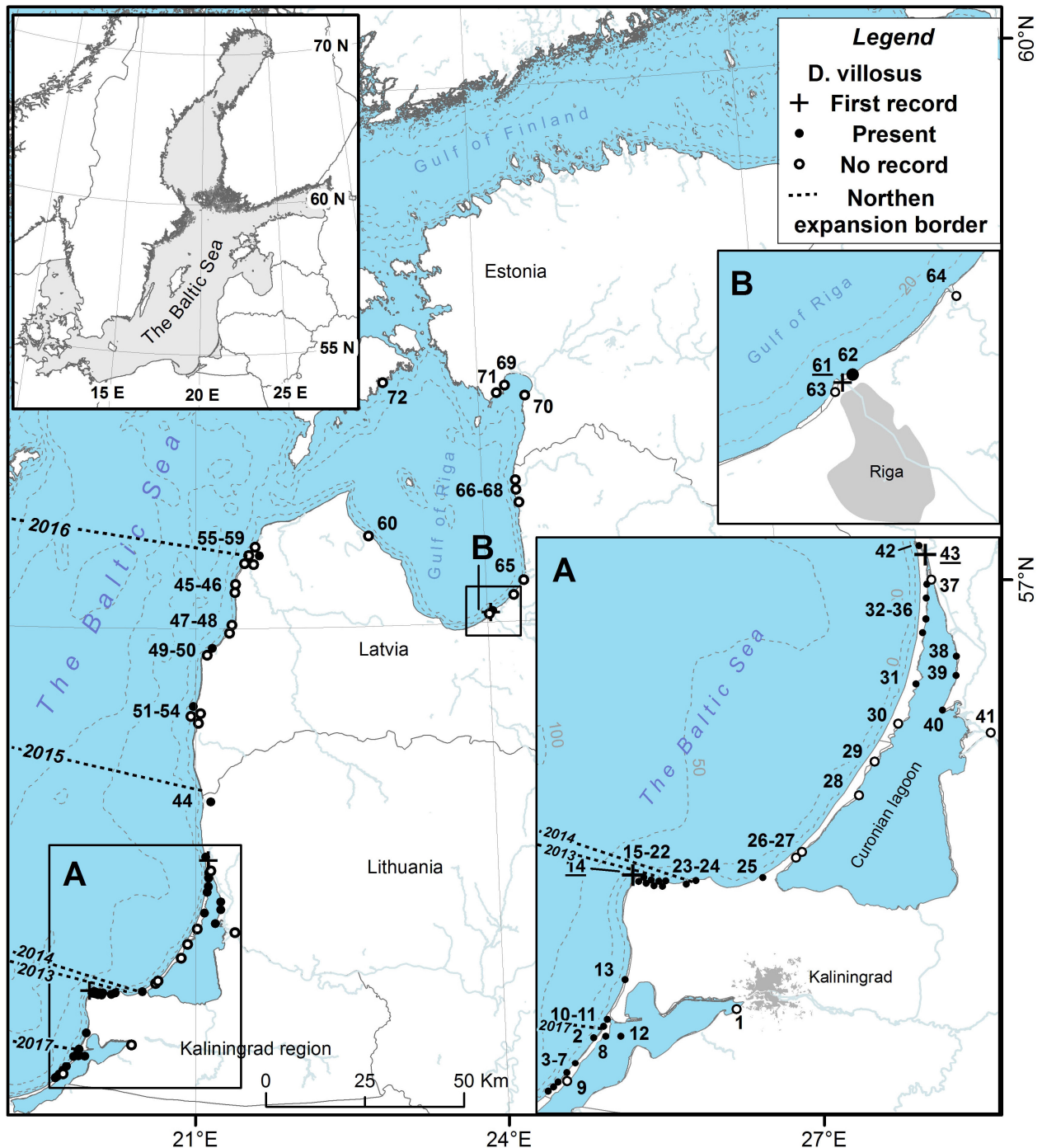
Figure 1. Study sites with *Dikerogammarus villosus* (filled circles) and where it was not found (open circles) along the south-eastern Baltic coast investigated during 2015–2017. All these sites were involved in analysis for influential factors of species distribution. First records for each country are shown with a cross. The most northern boundaries are shown for its range in each year. Note its entrance into the Vistula Lagoon in 2017 and its first appearance in Riga in 2015 (based on achieved material) for the station in inset B.

sites, "partly sheltered" for lagoon and "sheltered" for riverine sites and sites in the enclosed bays of the lagoons), annual average chlorophyll *a* concentration (μmol L⁻¹), summer average temperature (°C) and average salinity. Direction to the nearest port for sampling sites in open coastal waters was classified assuming a dominant transfer of water masses from south to north along the eastern Baltic coast (Leppäranta and Myrberg 2009). Salinity, temperature and chlorophyll *a* concentrations were derived from the

Copernicus Marine Environment Monitoring Service (CMEMS). Collinearity analysis between variables was based on linear correlation (r) and generalized variance inflation factor (GVIF) with the thresholds of r > 0.7 and GVIF > 10×(1/(2×Df) respectively (e.g. Dormann et al. 2013). None of predictors were found to fulfil these conditions and consequently all variables were used in the analyses. The pruning of the classification tree followed the rule of the smallest tree that has a mean cross-validation error (using 10 subsets) smaller than the sum of the cross validation mean for the largest tree and its standard deviation (Zuur et al. 2007).

The distribution of *D. villosus* was modelled using generalised linear modelling (GLM, binomial family and logit link function) to explore the species distribution in relation to the same set of seven predictors. Similar to regression trees, this method is designed to derive a set of important explanatory variables for analysed binary variable, but instead of threshold values of significant variables it provides information on the shape of response curve. GLM and associated analyses were carried out using freeware R 3.3.2 (http://www.r-project.org) and the package 'Rcmdr' ver. 2.3-2 (Fox 2016). Backward selection of the model variables following Akaike Information Criterion (AIC) and ANOVA test on significance of linear coefficients were used to select a final set of significant variables for the final model. The performance of the model was estimated using the area under the curve (AUC) of the receiver operating characteristic (Fielding and Bell 1997). Predictors were deemed significant at the $p < 0.05$ probability level. Partial residual plots of the reduced model were used for inspection of linearity between variables and interpretation of the main effects.

Results

Current distribution

Dikerogammarus villosus was most frequently collected along the marine coast of the Vistula Spit of the Russian Kaliningrad Region and within the Vistula Lagoon from a small semi-enclosed bay close to the sea entrance (Figure 1, Supplementary material Table S1: sites 2–8, 10, 11). It was not found within the Vistula Lagoon even close to the Polish border (Figure 1, sites 1, 9). By 2017 it had extended its range further within the Vistula Lagoon but still only within the region close to the sea entrance. It occurred on all coastal sites of the Sambian Peninsula (13–25). At sites 5–8 *D. villosus* was found attached to drifting *Fucus vesiculosus* and at sites 15–24 it was frequently found in abundance attached to floating, or near bottom drifting, *Furcellaria lumbricalis* and to the naturally attached *Polysiphonia fucoides* at 0–4 m depth. At sites 20–22 it was clearly seen to adhere to the wetsuits of divers when they left the water.

In Lithuania, *D. villosus* was first encountered within the port region of Klaipėda in 2015 (Figure 1: 42, 43; Šidagytė et al. 2016); and by the following

Figure 2. Shoreline of the Saka River Estuary in the fishing port of Pāvilosta, Latvia (left) where *Dikerogammarus villosus* was abundant; and its typical occurrence on the side of a fist-sized stone from the Saka Estuary (right). Photographs: Dan Minchin.

year it had become more widely spread within the adjacent Curonian Lagoon (31–40). By 2016 it was found in the region of the Neman River (40) and had not ascended the lower region of the river (40 and 41). The species was also absent from the southernmost part of the Curonian Lagoon within the Kaliningrad Region of Russia (sites 26–29) and Lithuania (30). While at the same time it was found close to the Latvian border to the north (44; Šidagytė et al. 2016).

In Latvian waters, *D. villosus* was seen in the Daugava River in vicinity of Rīga port during 2015 (Figure 1, site 61). In the following year it was collected within the ports of Liepāja (51), Pāvilosta (49) and Ventspils (59). In 2016 *D. villosus* was dominant among crustaceans along the Liepāja Port Estuary (51) adhering to the sides of immersed stones within wading depth and at also the Saka River Estuary in Pāvilosta (49) with > 20 specimens per fist-sized stone (Figure 2). These findings demonstrate a significant northward expansion from the Gulf of Gdansk and Lithuanian waters. However, *D. villosus* during 2016 was not found in 19 of the 24 studied sites in Latvia which included estuaries and river sections of the Riva, Užava, Inčupe, Gauja, Salaca, port of Roja and other sites (Figure 1, Table S1). Regular monitoring of the Estonian coast failed to reveal the presence of *D. villosus* despite the sampling 284 sites within suitable habitats during 2016 and 2017.

Pattern and factors affecting distribution

Current data indicates a lower species occurrence in the north-east of the study area, compared with the southern part, and shows a discontinuous distribution, especially within newly invaded areas along the Latvian coast (Figure 1).

The classification tree analysis identified mean summer chlorophyll *a* and temperature (although not shown in the tree plot, Figure 3), distance to the mouth of the nearest river or lagoon, and distance to the nearest port
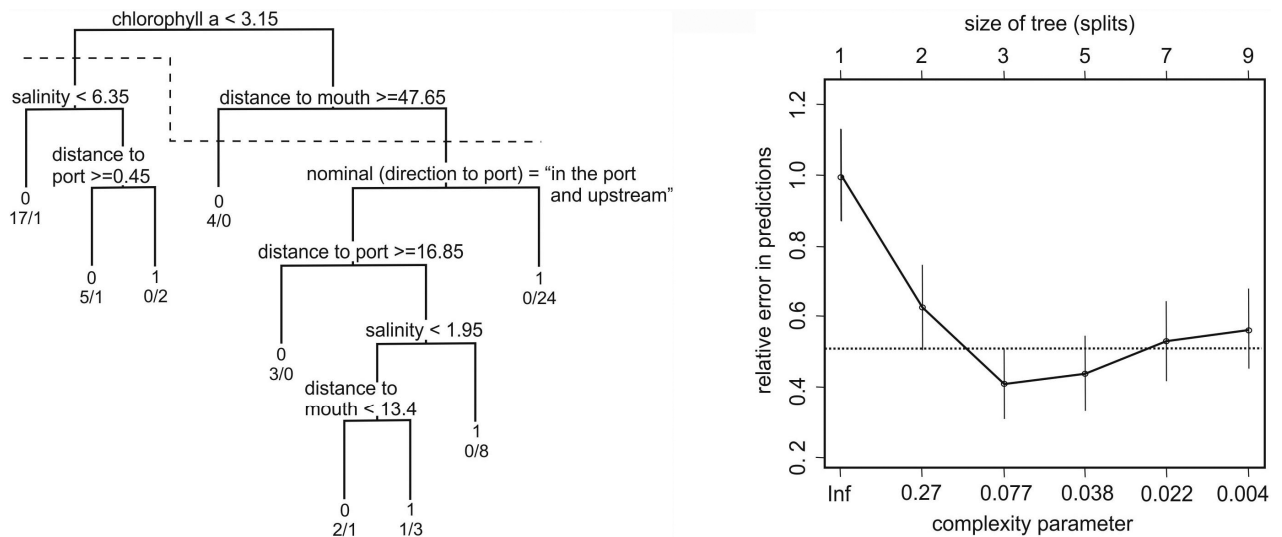
Figure 3. Graphical results of classification tree analysis. Classification tree (left): numbers below tree nodes indicate numbers of sites of species absence (indicated at the node as 0) / presence ((indicated at the node as 1); dashed line indicate tree size selection according to cross-validation results. Cross-validation results for classification tree (right): dashed line according to criteria of the tree pruning (see Material and methods for details); dots are the averages of the 10 cross-validations; vertical lines indicate standard deviation of cross-validations.

were the most important explanatory variables. Cross-validation of the model supports the reduction of the tree down to the two splits, based on average summer chlorophyll *a* and the distance to the mouth of the nearest river or lagoon (Figure 3). These two variables explain 56.2% of the total variance in the *D. villosus* distribution data. Average chlorophyll *a* concentration below 3.15 μmol L^{-1} characterised 69% (22 out of 32) of sites outside of the species distribution range, while larger chloro-phyll *a* concentrations and smaller than 47.6 km distance from the nearest river/lagoon mouth classified 90% (36 out of 40) species records.

The GLM with all environmental variables, resulted in an excellent fit with an AUC value 0.95 and relatively low residual deviance 37.10 (df = 62) compared to the null model deviance 98.92 (df = 71). Reduction of variables by backward selection using AIC values resulted in a model with a very similar AUC value (0.94) compared to the full model and no significant differences were found between the two models (Chi square = −2.06, p = 0.36). The final model had relatively high classification success (i.e. correspondence between observed and predicted findings) with 59 correctly classified cases out of 72, representing an 82% overall match between observed and predicted findings. Model classification success was relatively similar in both predicting species presence and absence, with a correct classification of 32 out of 40 sites where species were recorded and 27 out of the 32 sites lacking *D. villosus*.

Backward selection of the variables, when using AIC values and ANOVA test on significance of linear coefficients, provided essentially identical results on important variables for distribution of *D. villosus*, but backward selection largely resulted in higher number of marginal significance variables

Table 1. The GLM results: regression coefficients and their significance in the *Dikerogammarus villosus* distribution model after backward selection of environmental variables based on AIC criterion (left) and ANOVA results (right). Significant and marginally significant probabilities are in bold and italic, respectively. See material and methods for explanation of variables.

Variables / Statistics	Coefficients and their significance in the reduced model				Significance of coefficients according to ANOVA		
	Estimate	Std. Error	z value	Pr(>|z|)	LR Chi sq.	Df	Pr(>Chi sq.)
(Intercept)	5.210	3.845	1.355	0.175			
Chlorophyll *a*	0.481	0.236	2.037	**0.042**	12.595	1	**< 0.001**
Distance to Mouth	−0.092	0.050	−1.834	*0.067*	8.032	1	**0.005**
Distance to Port	−0.544	0.301	−1.809	*0.071*	10.253	1	**0.001**
Exposure					51.858	2	**< 0.001**
Exposure [exposed]	32.566	2633.854	0.012	0.990			
Exposure [sheltered]	−7.641	4.306	−1.774	*0.076*			
Direction to Port					6.847	2	**0.033**
Direction to Port [within port]	1.018	1.396	0.730	0.466			
Direction to Port [upstream from port]	−5.843	3.767	−1.551	0.121			

compared to the ANOVA test (Table 1). The final model identified the distribution of *D. villosus* being affected by five over seven tested predictors: mean summer chlorophyll *a*, distance to the mouth of the nearest river/lagoon, distance and direction to the nearest port, and exposure (Table 1). Partial residual plots indicate no violation of the linearity assumption for a relationship between *D. villosus* and significant predictors (Figure 4). The predicted probability of *D. villosus* was positively affected by chlorophyll *a*, while an opposite relationship was obtained for the distance from the nearest port and river/lagoon mouth. Similarly, higher probability of finding the species was obtained for ports and downstream areas compared to the upstream parts of invaded ecosystems. Sites exposed directly to the Baltic Sea coast were also found to favour finding the species with a significantly higher probability, however all such sampling sites were located in the southern part of the study area along the coast of Kaliningrad Region, Russia.

Discussion

Expansion and vectors

Our data confirms a rapid north-eastern expansion of *D. villosus* along the Baltic coastal and to estuarine waters. The species range extended 55 km northwards from Šventoji (site 44) to Liepāja Port (51) and a further 35 km to the fishing port of Pāvilosta (49). From Pāvilosta the distances to Ventspils (56) and Rīga (61) are 70 and 270 km, respectively, with a notable absence at Roja 120 km from Ventspils. It seems that this north-eastern expansion had occurred, within a few years at most. In the Curonian Lagoon *D. villosus* expanded its range within a year for approximately ~ 35 km to reach the delta of the Neman River (Figure 1).

The extension of *D. villosus* into Latvian waters was predicted following its occurrence in Klaipėda port (43) and in the Šventoji Estuary, in northern Lithuania, in 2015 (Šidagytė et al. 2016). While it had already appeared in
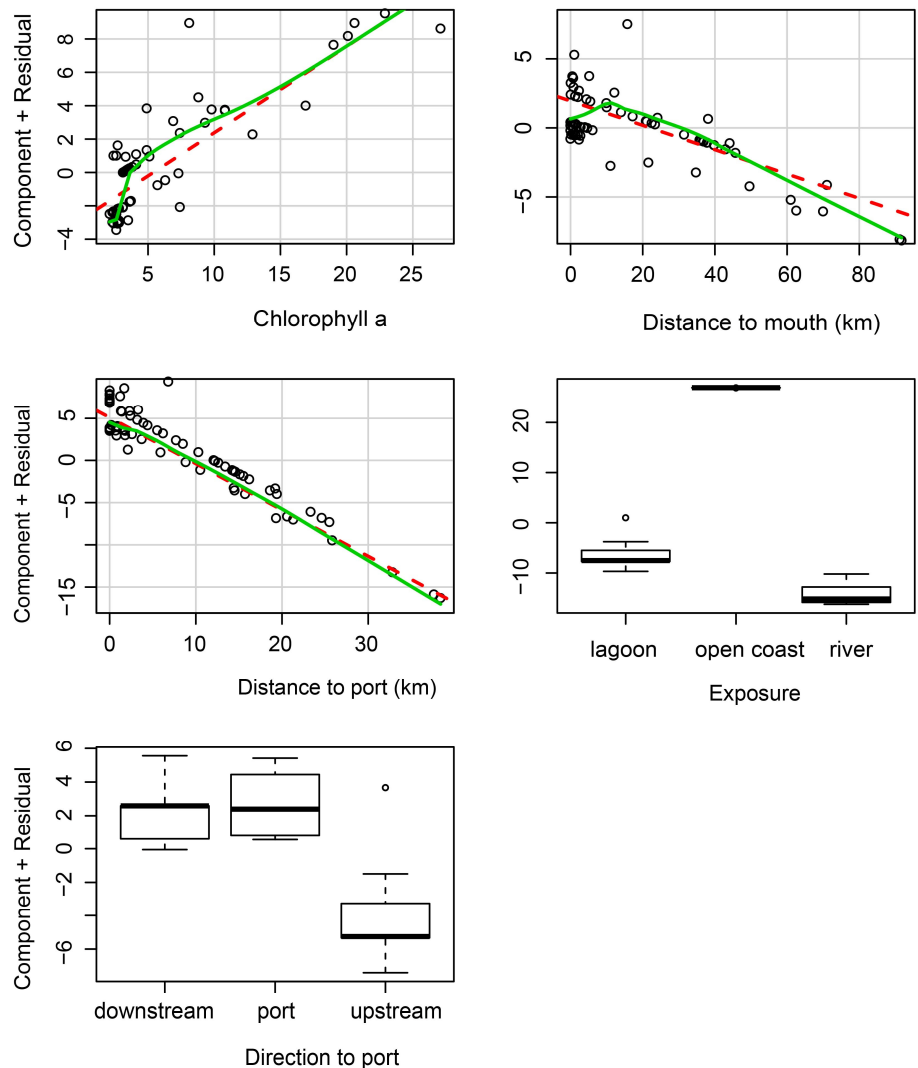
Figure 4. Partial residual plots for significant variables from reduced GL model. Dashed lines indicate the partial fit, assuming linearity in the partial relationship between presence/absence of *Dikerogammrus villosus* and given predictor; solid lines show a non-parametric locally weighted scatterplot smoothing (LOWESS) regression line. Distances in km.

2015 in the port region of Rīga (this account) following the earlier records in the Kaliningrad Region of Russia since 2013 (Gusev et al. 2017; Molchanova and Ezhova 2018). Discontinuous distributions of *D. villosus*, especially to the recently invaded Lithuanian and Latvian waters, clearly indicate that a "jump" dispersal is involved, and very-likely to be as a result of vessel transport. Ships can carry crustaceans in ballast water and several amphipod species have been found to frequent ballast water samples (Gollasch et al. 2002). This pathway is a very-likely reason for the introduction of another Ponto-Caspian amphipod *Echinogammarus ischnus* to the Great lakes of North America (Ricciardi and Rasmussen 1998). Since vessels moving between ports of the south-eastern Baltic Sea might have been spread *D. villosus* with ships' ballast water, we believe that it is more likely to have been transported by hull fouling, or with transported fishing equipment on commercial fishing vessels. The origin of

Table 2. Modes of spread, and the level of certainty of transmission (Minchin 2007), of *Dikerogammarus villosus* in Europe.

Transmission	Level of certainty	Reference
canals and navigable rivers	direct evidence	Bij de Vaate et al. 2002; Grabowski et al. 2007; Leuven et al. 2009
natural spread	direct evidence	Van Riel et al. 2011; Kobak et al. 2016, this study
vessels	very likely	Šidagytė et al. 2016; this study
vessels overland	very likely	Casellato et al. 2006; Martens and Grabow 2008; Madgwick and Aldridge 2011; Bącela-Spychalska et al. 2013; Rewicz et al. 2017
aquatic macrophytes and marine algae	very likely	Bącela-Spychalska et al. 2013; this study
fishing / recreational vessels, hull fouling	very likely	Anderson et al. 2014; this study
diving gear	possible	Bącela-Spychalska et al. 2013; this study
fishing equipment	possible	MacNeil et al. 2010; Bącela-Spychalska et al. 2013
flooding events	possible	Dobrzycka-Krahel and Rzemykowska 2010

the recently recorded populations in Latvia are presently unknown; but could involve a spread from the Szczecin (Gruszka and Woźniczka 2008), Vistula and/or Curonian lagoons. It is less likely to have arrived from elsewhere. The population arriving in the Gulf of Gdansk has been shown, using genetic methods, to have arrived from the Black Sea via the connections linking the Dnieper, Pripyat and Vistula rivers (Rewicz et al. 2015). The population in the eastern Baltic Sea is most likely to have spread along this route.

Other vectors of dispersal can also operate at a local scale as well as at a regional scale indicated by the attachment of *D. villosus* to *Fucus vesiculosus* (Table 2) which, except as drift, does not occur on the sea coasts of Poland or the Kaliningrad Region of Russia of Lithuania (HELCOM 2013). The arrival along the eastern Vistula exposed coast is very likely to have been with drifting plant materials. In this study *D. villosus* were associated with rafts of red or brown algae, actively growing macrophytes, fist-sized stones and flotsam. The red alga *Furcellaria lumbricalis* with many attached *D. villosus* were found in the Kaliningrad region many times on drift on beaches following strong onshore winds. *F. lumbricalis* occurs within most of the Baltic Sea, except for the northern part of the Gulf of Bothnia and within the Russian part of the Gulf of Finland (HELCOM 2017) and was found to raft as reported for the drift form *Furcellaria fastigiata aegagropila* in Danish waters (Austin 1960). It may be of little consequence whether angiosperms or algae are involved in amphipod transport. Amphipods within different world regions have been associated with floating algal rafts (Tully and Ó'Céidigh 1986; Ingólfsson 1995; Sano et al. 2003). Such transport may be more significant than currently thought especially for its occurrence with macrophytes elsewhere in its native region (Dedju 1967; Mordukhai-Boltovskoi 1969). *Dikerogammarus villosus* was observed to occur under the bark of floating logs in the northern Curonian Lagoon (this study). It is notable that *D. villosus* has been recorded attached to fishermens' waders, inflatable rubber craft, the hulls of boats (Truhlar and Aldridge 2015) and on wetsuits elsewhere (Bącela-Spychalska et al. 2013; and this study). Diving equipment, and even canoes,

may also spread *D. villosus* (MacNeil et al. 2010). Anderson et al. (2014) have indicated *D. villosus* can survive under damp conditions for 15 days. Overland transmission of leisure craft has been implicated in the colonisation of Alpine lakes in central Europe (Bącela-Spychalska et al. 2013). This species has been found to survive of up to six days within clusters of zebra mussels fouling such craft (Martens and Grabow 2008).

Although *D. villosus* may spread with coastal currents, seemingly with the secondary spread of rafting plant materials (Molchanova and Ezhova 2018), its long-distance spread is based upon evidence of its discontinuous distribution and absence in a number of estuaries and ports between Klaipėda and Rīga. This is most probably due to vessel transport. Its absence from the small coastal rivers and their estuaries on the Latvian coast may be because *D. villosus* normally colonises larger rivers and estuaries (Bij de Vaate et al. 2002). It might be that river size may also determine whether a species may become established, should it be spread with alongshore currents. In Latvia where the species was found in Pāvilosta and Liepāja it was abundant among stones. Its occurrence associated with stones is consistent with findings of Noordhuis et al. (2009) along lake shores. Kobak et al. (2015) indicated its preference for stony substrata, from gravels to large stones, over clusters of the zebra mussel *Dreissena polymorpha*; while juveniles were found to prefer macrophytes (Kobak et al. 2015). The small river estuaries of the Rīva, Saka or Užava had stones and macrophytes; and so may have been able to provide suitable habitats for this species.

Pattern and factors affecting distribution

The current pattern of *D. villosus* distribution, characterised by a north-eastward discontinuous occurrence, clearly suggests an expansion arising from transfers between ports with a subsequent local spread once having arrived in estuarine and lagoon waters.

The classification tree analysis and GLM generally confirm this current expansion pattern and indicate a relatively simple pattern for *D. villosus* distribution within the eastern Baltic Sea. Among the clearly influential factors of *D. villosus* distribution delivered as significant by both statistical methods was the distance of sampling sites to a river/lagoon mouth indicating an ongoing local expansion following an arrival. Occurrence of *D. villosus* was related to habitat productivity, assessed as chlorophyll *a* concentration, suggesting that the species currently occupies both mesotrophic and eutrophic environments. Although this result is determined by high species occurrence (58% of examined sites) within enclosed eutrophic lagoons (Curonian lagoon, Vistula lagoon), this pattern may change following the later invasion stages on entry to inland rivers of a lower trophic level. It is known for another Ponto-Caspian amphipod

Pontogammarus robustoides that there is an association between species occurrence and chlorophyll *a* concentration detected within Lithuanian freshwaters (Arbačiauskas et al. 2017).

Exposure was found to be highly significant by GLM, but not using classification trees. Interpretation of this factor is less straightforward, since statistical significance was clearly determined by method robustness to dataset features, i.e. distribution of sampling sites. All of the sampled sites (21) along the open coastline are situated in the southern part of the study area and all of those sites were found colonised by the species. This biased sampling with aggregation of exposed sites in one part of the study area does not permit a wider interpretation of this variable. The restriction of the interpretation of the importance of exposure for the occurrence of *D. villosus* relates to the type of the coastline. It is possible hard substrates along exposed coastlines may support colonies of mobile amphipods as efficiently as sheltered sites within lagoons and rivers, therefore exposure level can be efficiently masked. Furthermore, the effects of exposure are difficult to estimate due to species presence in drifting algae, which are common along the exposed coastlines. It remains unclear, if the species will occur at these exposed sites if not associated with drifting algae.

It would appear that the complex distribution within ports and recreational harbours in the Vistula and Curonian lagoons blurred the variable of distance between *D. villosus* occurrence sites and nearest port using the classification trees analysis. However, the GLM algorithm revealed this factor as being of similar marginal significance as the position of a site in respect to the nearest port. The later ("direction to the port") was the only variable which received controversial significance by two GLM methods and was not identified as significant by classification trees. Although this may also largely come from the complexity of multiple port positions in respect to a given sampling site, it can be influenced by bidirectional flow of riverine outflow and seawater intrusions in the lagoon systems (Zemlys et al. 2013). Depending on hydrological situation in freshwater systems, the later phenomena may support species expansion downstream or upstream from the port, therefore "direction" based variables may attain a lower statistical significance than those which account for distance.

Factors not examined in this study include depth and the type of substrate at the sampling sites. These habitat parameters may be of particular importance, although *D. villosus* will have been sampled over small distances along coasts, and is likely to contribute to some of the unexplained variance by the methods we used. It should be also noted, however, that these modelling results do not necessarily demonstrate a cause-effect relationship between the environmental variables and presence of *D. villosus*. It is likely that in course of increasing density and

adaptation, the species may expand its distribution into a broader environmental niche space, as has been found for other non-indigenous crustaceans within the Baltic Sea basin (Šidagytė et al. 2016).

Predictions for expansion

Climatic suitability is of prime interest when making species distribution projections. For example, Gallardo et al. (2012) determined that 60% of the area of Britain had a minimum suitability for *D. villosus*, and suggested a ≤ 10% bioclimatic suitability for species establishment in Latvia. In a separate study by Kurikova et al. (2016), a ten-point evaluation scale was produced, where levels of 7 or greater indicated a high probability of an establishment. Their assessment for *D. villosus* provided a low expectation level ranging from 3 to 6 for its spread to the northern Baltic Sea, and levels 2 to 4 for colonisation of British waters. In spite of this, the species is currently present in both Britain and Latvia. Furthermore, other Ponto-Caspian amphipod species such as *P. robustoides* or *Chaetogammarus warpachowskyi*, which originate from the same bioprovince as *D. villosus* have already become established within the Gulf of Finland (Berezina and Petryashev 2012).

Salinity is a further important environmental determinant for the distribution of amphipods. Salinities of up to 25 were tolerated by *D. villosus* in laboratory studies and the highest salinities in the entrance to the Baltic Sea attain this level; but there is a preference for 0.3 to 10 (Bruijs et al. 2001), with an optimal salinity 6 (Dobrzycka-Krahel et al. 2015). Others have indicated that the species is rarely found in salinities of ~ 0.5 (Grabowski et al. 2009). Since salinities of the eastern Baltic (range up to 7.8) are easily tolerated by *D. villosus*, the species could spread throughout coastal areas of the Baltic. This is very-likely based on recent expansions of the amphipods *P. robustoides* or *C. warpachowskyi,* from the same bioprovince now occurring within the Gulf of Finland (Berezina and Petryashev 2012).

Temperatures beneath winter-ice in the Curonian Lagoon are ~ 2 °C and laboratory studies indicate its tolerance to 34 °C (Kobak et al. 2017). As a result, there would appear to be few known restrictions to its further spread within the Baltic Sea.

Future predictions to the end of this century by Holopainen et al. (2016) suggest the increase of water temperature and tolerance to levels of salinity in the Baltic Sea might support *D. villosus* expansion within the northern Baltic Sea. Furthermore, Ponto-Caspian biota are highly adaptable to different environmental conditions as a result of their evolutionary historic challenges. Thus, rapid adaptation to the current and changing Baltic Sea conditions is likely to take place.

In summary, we predict *D. villosus* will invade the entire Gulf of Riga, presumably from the Rīga port area where it is already present, and the Gulf of Finland within years. In the future *D. villosus* will almost certainly colonise the majority of the coastal and estuarine waters of the eastern and northern Baltic Sea and will gradually expand upstream into rivers connected to the Baltic Sea. Following the expansion of this ecologically aggressive amphipod species, structural changes and alterations of local macroinvertebrate assemblages in invaded areas are likely to ensue.

Acknowledgements

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Supplementary material

The following supplementary material is available for this article:

Table S1. Sites examined showing occurrence of *Dikerogammarus villosus*.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2019/Supplements/AI_2019_Minchin_etal_Table_S1.xlsx